A reassessment of the predator responsible for Wakefield's 'Native Cat den' sub-fossil deposits in the Buchan district: Sooty Owl, not Eastern Quoll

Rohan J Bilney

PO Box 988, Bairnsdale, Victoria 3875
Email: rohan.bilney@gmail.com

Abstract
Norman Wakefield wrote two papers published in *The Victorian Naturalist* in 1960 that examined four sub-fossil deposits from caves in the Buchan district, East Gippsland, Victoria. Wakefield suggested that Eastern Quolls *Dasyurus viverrinus* were responsible for their accumulation in two caves, M-27 and M-28 (cave tag numbers). There is, however, limited evidence to support Wakefield's conclusion. Instead, there is convincing evidence that the Sooty Owl *Tyto tenebricosa* was responsible. This is based on the structural integrity of the sub-fossil bones, apparent digestive erosion on bones (indicating partial digestion and regurgitation by owls), characteristics of the caves, location of sub-fossils, surrounding habitat, body size-range of mammals within the sub-fossil deposits and known feeding ecology of all owl species. This is an important finding because analysis of the prehistoric and contemporary Sooty Owl diet can provide valuable information for our understanding of the small mammal palaeocommunity, recent declines and mammal conservation. (*The Victorian Naturalist* **129**(4) 2012, 138–143)

Keywords: *Tyto tenebricosa, Dasyurus viverrinus*, Norman Wakefield, mammal decline, Gippsland

Introduction

In 1960, Norman Wakefield wrote two articles published in *The Victorian Naturalist*, titled 'Recent mammal bones in the Buchan district – 1' and 'Recent mammal bones in the Buchan district – 2' (Wakefield 1960a, 1960b). Both articles examined mammalian sub-fossil remains excavated from four caves in the Buchan district of East Gippsland; three from the Pyramids area on the Murrindal River (Pyramids Cave (M-89), M-27 and M-28 (cave tag numbers)) and one from East Buchan (Mabel Cave). From the four caves, thousands of remains of small mammals eventually were identified, comprising approximately 44 species (Wakefield 1960a, 1960b, 1967, 1969, 1972). These articles provided significant information regarding the prehistoric distribution of small mammal species during the late Pleistocene and Holocene from south-eastern Australia.

Within the two papers from 1960 some of the material from M-27 and M-28 were only estimates of the number of individual animals found, and some morphologically similar species were not distinguished taxonomically (especially between Agile Antechinus *Antechinus agilis* and White-footed Dunnart *Sminthopsis leucopus*, and between Bush Rat *Rattus fuscipes* and Swamp Rat *Rattus lutreolus*). Although Wakefield conducted further examinations of the Pyramids Cave deposit after the initial 1960 publications, no further work was ever published on the sub-fossil material from M-27 and M-28. Following Wakefield's untimely death in 1972 (Willis 1973), much information about these two deposits was lost. Museum Victoria currently holds considerable material collected by Wakefield from these caves, but the original locality information is suspect for some material labelled as 'M-27 or M-28', 'M-28?', 'Buchan area' or 'Wakefield collection'. So it is difficult to assess whether the museum holds the complete collection. There is also a considerable volume of unsorted and unanalysed postcranial material from both M-27 and M-28. Despite these issues, a comprehensive taxonomic review and quantitative recalculation of the sub-fossil material from M-27 and M-28 would be of considerable value (especially the identification and calculation of the unsorted postcranial material). A reanalysis of the agent responsible for the accumulation of the sub-fossils in the caves also is warranted. This is an important aspect to understand because sub-fossil deposits are likely to represent a biased representation of the prehistoric mammalian community (Andrews 1990; Baird 1991; Yom-Tov and Wool 1997). If this bias can be better understood, then a more detailed understanding of how and why particular mammal species were present in the deposits can be understood (for example, may explain the absence, low or high representation of some species), thus providing a more comprehensive understanding of the prehistoric mammalian community. Most valuable, however, would be an ability to relate the sub-fossil deposits to the contemporary mammalian community in order to more comprehensively understand change over time and assess the condition of contemporary communities.

Original assessment of how sub-fossils accumulated in M-27 and M-28

Because of tbe position of the caves and the placement of sub-fossils in M-27 and M-28, the only way skeletal remains could accumulate to form large deposits is if they were transported there by a predator (an allochthonous deposit). At the time of Wakefield's publications in 1960, little was known about the feeding ecology of predators potentially responsible for the accumulation of sub-fossils. It was recognised that owls were most likely responsible for accumulating sub-fossil deposits in the Pyramids and Mabel caves because of the presence of numerous intact regurgitated pellets (Wakefield 1960a, 1960b). Wakefield considered that the Masked Owl *Tyto novaehollandiae* was most likely responsible for these two sub-fossil deposits primarily because it is larger than the Eastern Barn Owl *Tyto javanica* and more capable of capturing the larger prey species represented in these deposits (Wakefield 1960b). The relatively similar composition of the sub-fossil deposits within the Pyramids and Mabel caves suggests that the same predator was responsible. However, the composition of the M-27 and M-28 caves was considerably different (although similar to each other), containing much larger and many arboreal mammalian species, indicating that a different predator was likely responsible for these two deposits.

Wakefield considered that 'there is no reasonable doubt that both M-27 and M-28 were dens of the Eastern Native Cat' (currently named Eastern Quoll *Dasyurus viverrinus*) (Wakefield 1960a, p. 166). Wakefield (1960a) supports his claims by stating that quolls accumulate bones in stone shelters and often leave prey uneaten, citing papers by Fleay (1945) and Buckland (1954). The presence of both adult and juvenile Eastern Quoll bones in the deposit were assumed to be those of individuals that died in the deposit (Wakefield 1960a), rather than being prey remains of some other predator. Other terrestrial predators such as Foxes *Vulpes vulpes* and Tiger Cats (Spotted-tailed Quoll *Dasyurus maculatus*) were readily dismissed as likely contributors to the accumulation of sub-fossils, and no other likely predators (or agents) were considered (Wakefield 1960a, 1960b). Such a conclusion appears to have been based on speculation with little supporting evidence, primarily due to the unavailability at the time of ecological information on a range of native predators.

In light of recent ecological knowledge and an examination of remaining sub-fossil material from M-27 and M-28, a more accurate assessment of the predator responsible for these deposits can be made. There are several lines of evidence which suggest that Eastern Quolls were not the predator/agent responsible for the accumulation of sub-fossils in M-27 and M-28, and that a more likely predator was overlooked.

Why quolls were not responsible

Eastern Quolls were widespread and common in south-eastern mainland Australia until the early 1900s, when they underwent a major population crash, and are now extinct on mainland Australia (Menkhorst 1995; Jones 2008). They are now restricted to Tasmania where dietary studies reveal that they predominantly consume invertebrates, small to medium sized vertebrates and plant material (Blackhall 1980; Jones and Barmuta 1998; Jones 2008). Although Eastern Quolls are potentially capable of killing mammalian prey equivalent in size to many individuals in the sub-fossil deposits, they consume mainly small terrestrial vertebrates (Blackhall 1980; Jones and Barmuta 1998). The sub-fossil deposits in M-27 and M-28 contained a high proportion of large individuals (>500 g in body weight) and arboreal in habit, which is uncharacteristic of typical Eastern Quoll prey. Eastern Quolls would have had great difficulty dragging entire carcasses of prey into M-27 which (at least currently) has a steep rock scree approximately 1 to 1.5 m in height at the entrance of the cave, compounded with having to carry the prey considerable distances to get to the cave. The M-27 cave is also very large, open and spacious (several metres in height and width and extending deep into the cliff), and atypical of Eastern Quoll dens, which are characterised by discreet places that provide considerable shelter, such as small caves, rock piles, logs, stumps, dense vegetation, underground burrows, even under buildings (Godsell 1983; Jones 2008). Eastern Quolls are also scavengers (Jones 2008), so it appears unlikely that hundreds of prey remains would be left uneaten and relatively intact bones left to accumulate.

The home-range of Eastern Quolls is estimated to be typically less than 50 ha (Jones 2008). Therefore, if quolls were responsible for these sub-fossil deposits, their prey must have been captured in close proximity to the cave. Almost immediately in front of both caves (less than 20 m) is an ephemeral river, and immediately behind the cave is a sheer cliff, both of which potentially restrict the amount of habitat and area available for a terrestrial predator to hunt. It is highly unlikely that such a diverse range of prey species as represented within M-27 and M-28 (23-26 non-volant mammalian species) would have been available to Eastern Quolls in such a limited area. Overall, it appears that the predator responsible for these sub-fossil deposits was a much larger, wide ranging species, capable of transporting and consuming a diverse range of mammalian species over 1 kg in weight.

The much larger Spotted-tailed Quoll is capable of killing large and arboreal prey such as the species represented in the sub-fossil deposits (Belcher 1995; Glen and Dickman 2006; Belcher *et al.* 2007). However, there is good evidence that a mammalian predator was not responsible. Mammalian predators such as quolls usually kill their prey, particularly species such as rats, by biting the back of the skull or upper neck (Pellis and Nelson 1984; Pellis and Officer 1987; Jones 1997). Such a fatal bite, combined with subsequent consumption, would result in significant bone breakage and teeth marks on bones, particularly to the skull. At M-27 and M-28, however, reference was made to the large number of entire skulls of rodents, in particular 74 *Rattus* skulls (Wakefield 1960b). The photograph of bones on the floor of M-28 on page 169 (Wakefield 1960a) also highlights a large number of intact/unbroken bones. From recent visits to these sites (by the author), there still remain a significant number of intact/unbroken bones within both M-27 and M-28 caves. Bone material from these caves held at Museum Victoria also contains a large proportion of intact bones, further evidence that these deposits were not created by quolls.

Instead, evidence suggests that the predator/agent responsible for these sub-fossil deposits was not a mammalian predator, and that a more suitable candidate exists. Virtually all aspects of the M-27 and M-28 sub-fossil deposits are characteristic of an owl deposit (e.g. Baird 1991). Owls, particularly members from the genus *Tyto*, regularly ingest and regurgitate entire unbroken bones and intact skulls of their prey (Dodson and Wexler 1979; Kusmer 1990). They commonly roost in caves, and under suitable circumstances bones can accumulate over thousands of years, forming large sub-fossil deposits (Andrews 1990; Baird 1991). Owls are also among the main agents responsible for the accumulation of sub-fossils throughout Australia and the world (e.g. Andrews 1990; Baird 1991). In M-27 and M-28 all the bones are scattered around the floor directly below suitable perching ledges for roosting owls, while in M-27 bones also are located on ledges high above the floor of the cave. The large rocky scree at the entrance of the cave would have reduced accessibility to the caves by terrestrial predators, resulting in a relatively safe secluded position for an owl roosting site. The larger prey species with adult body weight typically exceeding 1 kg, such as Long-nosed Potoroo *Potorous tridactylus*, Eastern (Tasmanian) Bettong *Bettongia gaimardi*, Spotted-tailed Quoll and *Trichosurus* spp. are represented in the deposit mainly as juveniles, again typical of an owl deposit (Baird 1991). However, further evidence that an owl was responsible (at least for the majority of the deposit) from M-27 and M-28 is that numerous postcranial bones (especially limb bones), particularly of juvenile individuals, have mild digestive erosion on the proximal and distal ends, which indicate that the bones have been ingested and regurgitated, typical of owls (Dodson and Wexler 1979; Kusmer 1990; pers. obs.).

If an owl was responsible, which species?
Historically, at least five, possibly six, species of owl would have occupied the Buchan district. This includes three species of *Ninox*, the Southern Boobook *Ninox novaeseelandiae*, the Powerful Owl *Ninox strenua* and possibly the Barking Owl *Ninox connivens*. These *Ninox* species easily can be eliminated as agents responsible for sub-fossil deposits because they readily break bones of prey, rarely if ever roost in caves (except for the Boobook) and typically consume a wide range of vertebrate and invertebrate prey (e.g. Higgins 1999; pers. obs.). Although Southern Boobook regularly roost in caves, they predominantly consume mammalian prey of less than 100 g, while most of the prey remains in the sub-fossil deposits exceed this weight. On the other hand, the three species of *Tyto*, the Eastern Barn Owl, Masked Owl and Sooty Owl *Tyto tenebricosa* all consume predominantly mammalian prey, regularly roost in caves (or at least did in the past), regurgitate prey remains with limited damage to bones, and are all considered responsible for accumulating sub-fossil deposits elsewhere in Australia (e.g. Baird 1991). There is, therefore, strong evidence that a *Tyto* was responsible for the sub-fossil deposits, and although it is possible that all three species have used the M-27 and M-28 caves at some time over the last few thousand years, one species stands out as the most likely candidate. As each *Tyto* species varies considerably in regard to diet, habitat preference, roosting preferences and body size (e.g. Higgins 1999), a close examination of the composition of the sub-fossil deposits, the position of the cave in the landscape and the surrounding habitat, all help identify a single more suitable candidate.

Between 23 and 26 non-volant mammalian species were represented in the sub-fossil deposits from M-27 and M-28. This is likely to represent most non-volant small mammal species (less than 2 kg in either adult or juvenile body weight) that inhabited the area, except perhaps the Yellow-bellied Glider *Petaurus australis*, Water Rat *Hydromys chrysogaster* and (the large) Red-bellied Pademelon *Thylogale billardierii* (e.g. Menkhorst 1995). The two sites combined contained five arboreal (26%), at least seven scansorial (29%) and 11 terrestrial (45%) species. These species represented a wide range of body sizes, from species under 50 g through to and over 1 kg in adult body weight, most of which were represented by juveniles (Wakefield 1960a).

The smallest *Tyto* species, the Eastern Barn Owl, can easily be eliminated at least from being the major accumulator of the sub-fossil deposits because this owl typically weighs 300-400 g and predominantly consumes terrestrial mammal species of less than 200 g in body weight (Baird 1991; Higgins 1999). The larger Masked Owl weighs up to 900 g and would be capable of consuming the species present in this deposit; however, they also predominantly consume terrestrial species and only occasionally scansorial and arboreal species (Higgins 1999), but these sub-fossil deposits contained a high proportion of arboreal and scansorial prey (56% combined). The upper size limit of prey captured by mainland Masked Owls is poorly understood, but it appears unlikely that they would have consumed such a large proportion of larger prey as represented in the M-27 and M-28 deposits. So although it is possible that the Masked Owl may have been partially responsible for the sub-fossil deposits, a more likely candidate is the Sooty Owl.

Why the Sooty Owl was likely responsible
There is strong evidence to suggest that the predator predominantly responsible for the M-27 and M-28 sub-fossil deposits was the Sooty Owl. The Sooty Owl was dismissed by Wakefield as a possible predator responsible for the Pyramids and Mabel caves sub-fossil deposits only because very little was known about its ecology in the 1960s (Wakefield 1960b). However, knowledge of the ecology and feeding habits of the Sooty Owl has increased considerably since the early 1990s (Debus 1994; Kavanagh 1997; Higgins 1999; Bilney *et al.* 2006; Bilney *et al.* 2010; Bilney *et al.* 2011). The Sooty Owl is not only the largest of the

Tytonidae on the mainland (females regularly weighing up to 1.2 kg) it has also the most generalist diet of any *Tyto* species and is capable of consuming virtually all terrestrial, arboreal and scansorial mammalian species available up to approximately 1.3 kg in size (Kavanagh 1997; Higgins 1999). Such a size range incorporates the prey size of all remains in the M-27 and M-28 caves. Sooty Owls also consume a high proportion of arboreal prey (Bilney *et al.* 2006, 2011a), a feeding trait unlike the other *Tyto* species in the area (Higgins 1999). As the Sooty Owl is a large predator, it rarely consumes small terrestrial prey, and focuses primarily on prey with a body mass in the range of 50 to 900 g (Bilney *et al.* 2011b).

The composition of the sub-fossil deposits from the M-27 and M-28 also closely resembles the composition of sub-fossil deposits in the Mitchell River catchment (about 80 km to the west of Buchan) that are also attributed to the Sooty Owl (see Bilney *et al.* 2010).

Sooty Owls are strongly associated with rainforest and wet forest types in East Gippsland (McIntyre and Henry 2002; Bilney *et al.* 2011) and regularly roost in caves or rock shelters protected under the forest canopy (such as rainforest), usually with an easterly or southerly aspect (Bilney *et al.* 2011). Both the M-27 and M-28 caves are situated under the canopy of Gallery Rainforest, dominated by Kanooka *Tristaniopsis laurina* and Muttonwood *Myrsine howittiana*, face east, and are situated about 20 m from the Murrindal River. All characteristics of the M-27 and M-28 caves are characteristic and suitable Sooty Owl roosting sites.

The importance of identifying a Sooty Owl sub-fossil deposit

Understanding that the sub-fossil deposits from M-27 and M-28 are predominantly prey remains generated by the Sooty Owl can provide important information about the prehistoric mammalian community. As Sooty Owls are capable of overcoming and consuming all mammalian species up to approximately 1.3 kg in weight, this gives confidence that most species that occupied the area surrounding the Pyramids area during the late Holocene are likely to be represented in the deposits. In other words, it is unlikely that there would be many small mammal species that are absent from the deposit.

The other important issue is that because the Sooty Owl is still widespread in East Gippsland, analysis of its contemporary diet can be compared to its prehistoric diet (from the sub-fossil deposits) potentially revealing significant information about the extent of small mammal decline overtime, especially following European settlement (Bilney *et al.* 2010). This technique provides virtually the only ability we have to relate contemporary mammalian community composition to a prehistoric context, therefore potentially providing an assessment of the current condition of mammal communities vital to the understanding of mammal conservation and appropriate land management practices (Bilney *et al.* 2010).

Conclusion

There is strong evidence that the Sooty Owl, rather than the Eastern Quoll (as originally speculated by Wakefield) was responsible for the accumulation of at least the majority of the remains in the sub-fossil deposits excavated from the caves M-27 and M-28. This is potentially an important aspect for future researchers to acknowledge when referring to Wakefield's 1960 papers. The implication that the Sooty Owl was responsible for the accumulation of these sub-fossils has important ramifications for our understanding of small mammal decline and small mammal conservation.

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